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REVIEW

The mechanisms underpinning lateral gene transfer between grasses

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Societal Impact Statement

Lateral gene transfer (LGT) refers to the transmission of genetic material without sexual reproduction. LGT is widespread in a number of plant species, including grasses. But how these genes of foreign origin got there is presently unknown. In this review, we show that transformation techniques used to genetically modify organisms could occur in the wild and be responsible for the frequently observed grass-to-grass LGTs. The distinction between natural evolutionary processes and genetic engineering might be arbitrary, and its validity will be further debated as agricultural biotechnology becomes more widely used and examples of “natural genetic engineering” through LGT increase.

Summary

Lateral gene transfer (LGT) is the transmission of genetic material among species without sexual reproduction. LGT was initially thought to be restricted to prokaryotes, but it has since been reported in a wide range of eukaryotes, including plants. Grasses seem to be particularly prone to LGT and frequently exchange genes among species. However, the mechanism(s) facilitating these transfers in this economically and ecologically important group of plants are debated. Here, we review vector-mediated, direct tissue-to-tissue contact, wide-crossing and reproductive contamination LGT mechanisms and discuss the likelihood of each in light of recent studies. Of particular relevance are transformation approaches that require minimal human intervention to transfer DNA among grasses in the lab that could mimic the mechanisms facilitating grass-to-grass LGT in the wild. These approaches include relatively simple techniques, such as pollen tube pathway-mediated transformation, that take advantage of the permeability of the reproductive process to introduce alien genetic material from a third individual into an embryo. This process could be easily mirrored in the wild where pollen from one species lands on the stigma of another, acting as a source of alien DNA that can ultimately contaminate the reproductive process. This contamination is likely to be prevalent in wind pollinated species such as grasses, where the rates of illegitimate pollination will be high. In conclusion, plant transformation methods requiring minimal intervention are likely paralleled in the wild where they act as the mechanism underpinning LGT between distantly related grass species.

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adaptation, genetically modified, horizontal gene transfer, introgression, Poaceae

1 | INTRODUCTION

Lateral gene transfer (LGT) refers to the process by which alien genetic material is acquired without sexual reproduction. LGT facilitates genetic exchanges over much broader evolutionary distances (even between prokaryotes and eukaryotes) than through hybridization and introgression. LGT has been extensively studied in prokaryotes, where both the mechanisms (transformation, conjugation, and transduction) and consequences are well known (Hall et al., 2020). The rapid spread of genetic material between species can have drastic adaptive impacts. For example, in prokaryotes, LGT allows the rapid spread of antibiotic resistance through plasmid transmission (Ochman et al., 2000). More generally, LGT can act as a source of novel genetic material, and the encoded proteins may have optimized or unique functions. LGT can even unlock novel routes to develop phenotypes outside of those readily achievable through descent with modification alone. The evolution of specific traits may be unlikely in lineages that do not possess the required genetic precursors (Blount et al., 2012). LGT has the potential to bypass this problem by expanding a species gene pool beyond its reproductive boundaries. While the existence of LGT in eukaryotes was originally controversial, it is now a question of “how much” rather than “if” it occurs (Van Etten & Bhattacharya, 2020).

The advent of high-throughput sequencing and advances in phylogenomics have led to an ever accumulating number of LGTs reported in a broad range of eukaryotes. These LGTs are typically detected through phylogenetic incongruences between the species and gene tree topologies. In some unicellular eukaryotes, about 1% of predicted genes were acquired laterally, with most of them being bacterial in origin (Fan et al., 2020; Matriano et al., 2021). In multicellular organisms, there are unequivocal examples in animals (Bryon et al., 2017; Undheim & Jenner, 2021), fungi (Duarte & Huynen, 2019; Murphy et al., 2019; Szöllösi et al., 2015), and plants (Wickell & Li, 2020). Among plants, LGT seems especially prevalent between parasites and their hosts, where direct tissue contact via the feeding structures known as haustoria facilitate genetic movements (Vogel et al., 2018; Xi et al., 2012; Yang et al., 2019; Yoshida et al., 2019). Among non-parasitic plants, LGTs have been reported in ferns (Li et al., 2014) and between numerous members of the grass family (Christin et al., 2012; Dunning et al., 2019; Hibdige et al., 2021; Mahelka et al., 2021, 2017; Park et al., 2021; Prentice et al., 2015; Vallenback et al., 2008; Wu et al., 2022). The genes transferred among grasses include those with functions associated with disease resistance, abiotic stress tolerance, and photosynthesis (Christin et al., 2012; Dunning et al., 2019; Hibdige et al., 2021). Biochemical assays have confirmed that some of these transfers are adaptive (Phansopa et al., 2020), and population genomics shows that they spread rapidly through a population under positive selection (Olofsson et al., 2019).

Successful LGT requires not only the acquisition of foreign genetic material but also its assimilation into the germ line so that it can be spread from the individual that originally acquired it. In plants, any LGT into the ovules, pollen, or embryo would be the easiest route and mirror certain transformation techniques. In addition, LGT acquired by meristematic cells that give rise to inflorescences and gametes would also be inherited by the progeny. Unlike in animals, the germline and soma are not clearly separated in plants, and many species are able to reproduce vegetatively (Su et al., 2021). Individuals from clonal populations present high degrees of genetic variation among them, which indicates the prevalence of somatic variants (Haddadchi et al., 2013; Yu et al., 2020). Importantly, new somatic mutations can increase in frequency during bottlenecks generated by stolons and rhizomes, becoming fixed in subsequent clones (Yu et al., 2020). Vegetative growth is widespread in grasses, so we consider that LGT integrated in meristematic cells can be transmitted to the next generations.

Several mechanisms have been hypothesized for LGT among non-parasitic plants, such as grasses (Christin et al., 2012; Dunning et al., 2019; Hibdige et al., 2021; Park et al., 2021; Roulin et al., 2009; Soucy et al., 2015; Sun et al., 2013; Wickell & Li, 2020; Wu et al., 2022). Likewise, mechanisms allowing the transfer of genes among species are well established in the context of plant transformation and hybridization. In this manuscript, we review the mechanisms known to mediate interspecific gene exchanges based on experimental systems and discuss their application to grass-to-grass LGT. We first review the mechanisms that have been suggested for the entry of foreign DNA into grass cells and then briefly discuss the mechanisms allowing their chromosomal integration. Our efforts help identify the most likely scenarios, and demonstrate that viable mechanisms exist, removing an obstacle to the widespread acceptance of LGT by plant biologists.

2 | HOW DOES EXOGENOUS DNA ENTER FOREIGN CELLS?

2.1 | Vector-mediated

Bacterial and viral vectors are often perceived as the most likely mechanism behind eukaryotic gene transfers, perhaps because they frequently exchange genes through their infection cycle (Figure 1). The role of these vectors in eukaryote LGT would be facilitated by the ubiquitous presence of bacterial and viral plant pathogens that infect a broad range of hosts and with which they can exchange DNA (Feschotte & Gilbert, 2012; Gilbert & Cordaux, 2017). DNA is exchanged through processes such as endogenization, where retroviruses insert genetic material into the host genomes to complete their

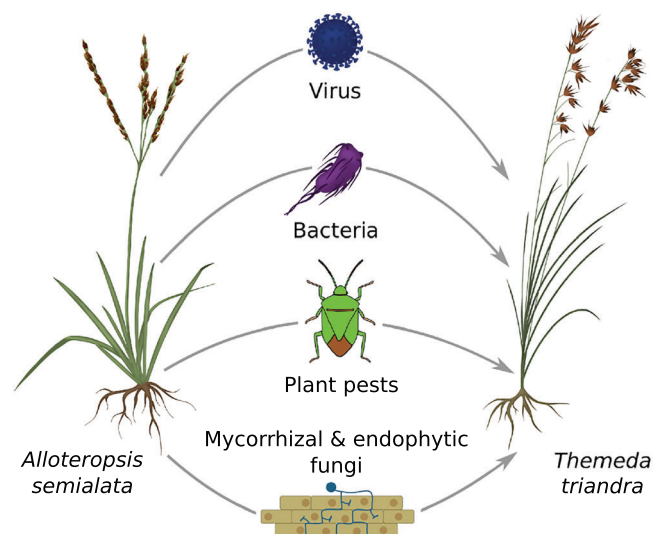


FIGURE 1 Potential agents of vector-mediated transfers between grasses. Grass species depicted were involved in a known case of lateral gene transfer (Dunning et al., 2019).

life cycle (Weiss, 2006). While originally reported in retroviruses, endogenization is now known to be pervasive among a wide variety of viruses (Feschotte & Gilbert, 2012). The precise molecular mechanism through which endogenization happens is not known, although retrotransposons seem to be involved in the process (Geuking et al., 2009; Horie et al., 2010). The transfers are not unidirectional, meaning that viruses can integrate host DNA into their own genome, using either their own machinery (retroviruses) or retrotransposon/host machinery (Gilbert et al., 2016). Some viruses acquired up to 30% of their entire genome from eukaryotes (Gilbert & Cordaux, 2017), representing ~30–70 kb overall (Morissette & Flaman, 2010). Therefore, it is possible that a virus acquires DNA from an initial host and then transfers it to another species as part of a subsequent infection. Generalist viruses have a broad range of hosts and could potentially infect many grass species (Ingwell & Bosque-Pérez, 2015), thereby passing DNA fragments from one species to another. Virus-mediated lateral transfer of approximately 1 kb regions of chromosomal DNA between plant species has been documented in real time (Catoni et al., 2018). However, it is unlikely that a virus would be able to act as a vector for the much larger fragments of DNA passed between grasses that can be over 400 times larger (Mahelka et al., 2021).

Genes of bacterial origin are often found in eukaryotic genomes (Fan et al., 2020; Matriano et al., 2021). In fact, certain bacteria are so successful in transforming plants that scientists have used them in the laboratory for decades (Horsch et al., 1985). This process is reliant on the *Agrobacterium tumefaciens* bacteria, a pathogen from the Rhizobiaceae family that causes crown gall disease in plants (Smith & Townsend, 1907). *A. tumefaciens* transfers, integrates, and expresses a set of genes into the infected plant via a plasmid, resulting in the gall formation (Hoekema et al., 1984). This ability has been manipulated to replace the bacterial loci with genes encoding desired proteins

(Horsch et al., 1985). *A. tumefaciens* and its close relative *Agrobacterium rhizogenes* have also naturally transferred their genes to a large number of species in the wild (Intrieri & Buiatti, 2001; Kyndt et al., 2015; Matveeva et al., 2012; Matveeva & Otten, 2019). Yet the transfers do not seem to be reciprocal, since no gene of plant origin has been found in the *A. tumefaciens* genome (Wood et al., 2001). *Agrobacterium* is thus responsible for LGT from bacteria to plants, but it is less likely to be a vector in the more complex scenario where DNA is ultimately moved between plants via an intermediary. Furthermore, grasses are not natural hosts of *Agrobacterium* (Conner & Dommissé, 1992; Lowe et al., 2016), and establishing lab-based transformations in this family is challenging (Nguyen et al., 2020). Other bacteria might be capable of naturally transforming grasses, but this is presently unreported. It should also be noted that symbiotic bacteria, and not just pathogens, have been associated with LGT in plants, for example, the emergence of land plants is correlated with the acquisition of stress tolerance genes from soil bacteria (Cheng et al., 2019). However, there is no evidence that symbiotic bacteria can facilitate transfers between plant species.

Another potential vector could be arbuscular mycorrhizal fungi, which are mutualistic symbionts that develop intimate and long-term associations with plant roots (Field et al., 2015). Plants and mycorrhizal fungi share a wide range of molecules, from sugars and other nutrients to mRNAs (Field et al., 2015; Wong-Bajracharya et al., 2022). Some mycorrhizal fungi have been donors and recipients of LGT from plants and bacteria (Sun & Huang, 2018). Although movements of DNA between plants in this symbiotic association have not been described yet, we cannot rule out their existence and material to support or refute their involvement as a vector for LGT is missing. There is more evidence that endophytic fungi could act as the vector of grass-to-grass LGT as it has been shown that they can both acquire and transmit alien DNA. *Epichloë* endosymbiotic fungi have acquired a bacterial insect toxin gene, which confers insect resistance to their grass host (Ambrose et al., 2014), and *Epichloë* has passed a gene for disease resistance to a close relative of wheat (Wang et al., 2020).

Plant feeding arthropods could also mediate the transfer of DNA between plants. At its simplest, this process could involve contaminated feeding mouthparts transferring DNA between tissues of different species. Of particular interest would be insects that directly feed on plant seeds, as this may offer a route to introduce genetic material into the germline of the recipient. Hemipterans belonging to the Lygaeidae are commonly referred to as seed bugs and possess needle-like piercing mouthparts with which they use to extract nutrients (Burdfield-Steel & Shuker, 2014). Several species in this group are generalists, and it is possible that they could transfer DNA between species as they feed. Although there is no direct evidence for this, Sap feeding insects are known to frequently act as vectors for plant pathogens; for example, maize streak virus is spread by a leafhopper (Storey, 1924). It is also possible that insect-mediated transfers involve the more convoluted route of being incorporated into the herbivore genome before being subsequently passed on to the recipient plant species. It has been hypothesized that LGT contributes to the evolution of arthropod herbivory (Wybouw et al., 2016), and genes of

plant origin have been detected in the genomes of plant pests such as the whitefly (Xia et al., 2021). However, whether these acquired genes can then be passed on to a third species is unknown, and no flanking insect DNA has been detected in the documented grass-to-grass LGTs (Dunning et al., 2019; Mahelka et al., 2021).

We know that viruses, bacteria and fungi are able to introduce their own genetic material into their host, but whether they are able to act as a bridge between hosts remains unclear. There is no obvious signal of vector-mediated transfer in the fragments of DNA moving between grasses, with no DNA from a “third party” detected (Dunning et al., 2019; Mahelka et al., 2021), although this signal may only be temporary as the integrated fragments erode over time (Dunning et al., 2019; Olofsson et al., 2019). Furthermore, the transferred fragments can be relatively large, which makes vector-mediated transfer unlikely to explain the frequently observed grass-to-grass LGT. Laterally acquired fragments over 400 kb in length have been detected in the *Hordeum bogdanii* genome (Mahelka et al., 2021), which is larger than most viral genomes. In conclusion, it is unlikely that the observed grass-to-grass LGTs are vector-mediated given the lack of signal in the recipient's genome, their unwieldy size, and the fact that grasses are not a natural host for *Agrobacterium* bacteria.

2.2 | Natural grafts

No parasitic grass has been reported to date (Nickrent, 2020), but it is still possible that the transfers occur through direct contact. Inosculation is the spontaneous junction of plant tissues from two different individuals that later continue their growth as a whole, a term that is generally applied to trees. When performed artificially, inosculation is named grafting. Grafting is commonly used in plant breeding for a wide range of applications usually related to increasing biotic and abiotic stress tolerance (Melnik & Meyerowitz, 2015). Initially, the stock (root system) and the scion (aerial portion of the plant) were thought to conserve their genetic integrity. However, genetic data have been used to show that chloroplast, mitochondrial, and nuclear genomes can be asexually transferred between the stock and the scion (Fuentes et al., 2014; Gurdon et al., 2016; Stegemann & Bock, 2009). Subsequent detailed observation of the cells forming the junction of the grafting revealed that small, dedifferentiated chloroplasts were transferred through cell wall pores (Hertle et al., 2021). These organelles carried plastid DNA, and their movement was observed using live imaging, representing the ultimate proof of lateral gene transfer in plants.

Grafting monocotyledonous plants was previously thought to be impossible due to the absence of a vascular cambium, the meristematic tissue that promotes secondary growth in other groups of plants (Rasool et al., 2020). However, based on the hypothesis that embryonic tissues are essential for grafting, Reeves et al. (2022) developed a novel method for grafting monocot embryos and grafted several grass species. The inosculation between grasses from different species in the wild could act as a junction for DNA transfer although this is unlikely to occur between embryos due to the protective seed

coat. Natural grafting could occur between mature tissues such as rhizomes, but this has not as yet been demonstrated.

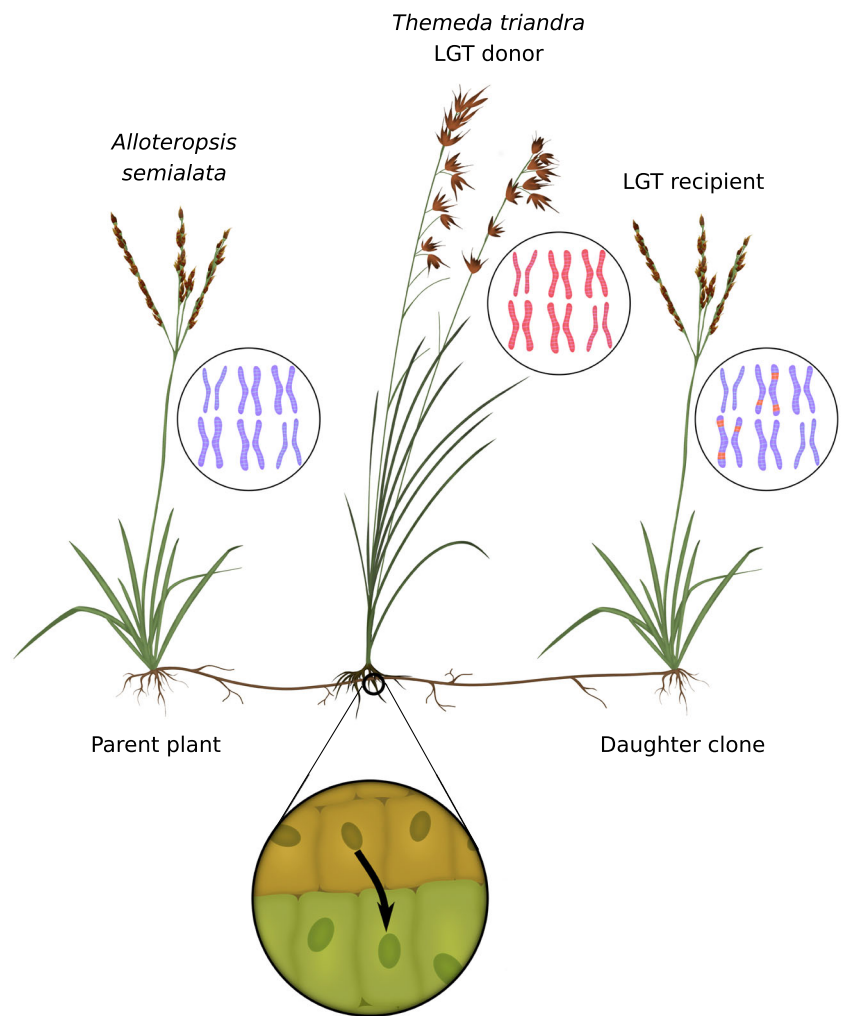
Previous studies investigating the distribution of grass-to-grass LGTs have shown that species capable of producing rhizomes and asexually propagating themselves had a significant increase in the number of LGT detected in their genomes (Hibdige et al., 2021). This signal of increased LGT in species with rhizomes could mean that LGT in grasses takes place during vegetative reproduction, for example through root-to-root inosculation in dense multispecies clumps (Figure 2) (Dunning et al., 2019). Alternatively, the positive correlation between the number of LGT and the presence of rhizomes may be a result of a reduced efficacy of selection to purge neutral or deleterious mutations in asexual species (Muller, 1964). The ability to propagate asexually through rhizomes would therefore increase the rate of LGT retention rather than the rate of acquisition. In any case, LGT is not restricted to grasses with rhizomes, meaning that even if a mechanism to support root-to-root inosculation was demonstrated, it still would not be able to explain the large number of LGTs recorded in non-rhizomatous grass species.

2.3 | Wide crosses

It is possible that the phylogenetic discordance used to infer lateral gene transfer is actually driven by rare hybridization events between highly divergent species, for example, different subfamilies. Grasses are a diverse family of plants that include over 11,000 species that diversified over the last 100 million years (Huang et al., 2022; Soreng et al., 2017). Distantly related species from different subfamilies that diverged up to 80 Mya have been manually crossed and used to obtain partial hybrids including both oat and wheat crossed with maize (Laurie & Bennett, 1986; Riera-Lizarazu et al., 1996). In most cases, embryo rescue is required to recover haploid or partial hybrids resulting from wide interspecific crosses, and the yield of hybrid plants is low, around 3% of all recovered embryos (Riera-Lizarazu et al., 1996). These partial hybrids acquired a complete set of chromosomes from the mother plant and an incomplete set of chromosomes from the donor pollen. Often, these alien chromosomes are eliminated during the first days of embryo development (Laurie & Bennett, 1986), but sometimes these hybrids developed and were even partially fertile, transmitting the donor chromosomes to their progenies (Kynast et al., 2001).

Wide crosses require successful growth of heterospecific pollen tubes, and numerous studies have shown that heterospecific pollen can usually grow to a certain extent in other grasses' styles (Heslop-Harrison, 1982; Lausser et al., 2010; Reger & James, 1982). Indeed, the more closely related the species are, the more likely this would happen (Lausser et al., 2010). This trend mirrors the pattern of LGT we see in the grasses, with the amount of LGT increasing with phylogenetic relatedness, although this is also confounded by biogeography (Hibdige et al., 2021). The non-syntenic insertion of LGTs into the recipients' genome and their coexistence with vertically acquired copies argues that they were not acquired through straightforward hybridization with sexual reproduction and chromosomal

FIGURE 2 Cartoon illustrating the hypothesized root-to-root inosculation mechanism of lateral gene transfer (LGT). Foreign DNA is transferred into the rhizome through a natural graft, pictured in the expanded circular cut-out. When a daughter clone is generated, the foreign DNA is incorporated into somatic and germline cells. The species depicted were involved in a known case of LGT (Dunning et al., 2019), with DNA of the recipient species shown in blue and the donor in red.



recombination (Dunning et al., 2019; Hibdige et al., 2021; Mahelka et al., 2021). However, the movement of genes could have occurred during the transient cohabitation of chromosomes in the nucleus of wide crosses. The occurrence of wide crosses has not been documented to occur naturally between grass crops, possibly due to the necessity for embryo rescue for species separated by greater taxonomic distances such as crosses between different subfamilies, evolutionary distances we frequently see LGT bridge. It therefore appears unlikely that wide-crosses are the source of LGTs in grasses.

2.4 | Reproductive contamination

Reproductive contamination as a result of illegitimate pollination has been hypothesized as a potential mechanism for grass-to-grass LGT (Christin et al., 2012). Such LGTs would effectively be natural transgenic events, with particular parallels to transformation methods without the requirement for in vitro culture. Here, we focus on two techniques, called repeated pollination and pollen tube pathway-mediated transformation, that could happen in nature without human intervention. This experimental evidence suggests that reproductive barriers can be overcome in the wild, leading to LGT.

2.4.1 | Repeated pollination

Repeated pollination was developed to generate interspecific hybrids in rice, aiming to introduce traits of agronomic interest from wild relatives (Liu et al., 1999). However, we have chosen to classify these plants in this review as transgenic plants as the natural reproductive process is effectively contaminated with DNA from a third individual. In this procedure, emasculated rice stigma from a cultivated variety were first treated with pollen from a wild relative from the same subfamily (*Zizania latifolia*) that diverged from rice ~46 Mya (Huang et al., 2022). After 48 h, a second pollination with pollen from the same rice cultivar was performed (Figure 3a). Seedlings resulting from this repeated pollination were inspected and a very low percentage showed distinctive phenotypes. These altered plants were self-pollinated repeatedly to obtain recombinant inbred lines, which are genetically stable. Surprisingly, the vast majority of their genetic material was from the rice cultivar, but they contained <0.1% of genomic DNA from *Z. latifolia* (Shan et al., 2005). Most of the identified transferred sequences were transposable elements (TE), which caused genomic rearrangements beyond their insertion. A similar study using a different rice accession also found mobilization of host TEs after repeated pollination experiments, but no alien genomic DNA (Wu

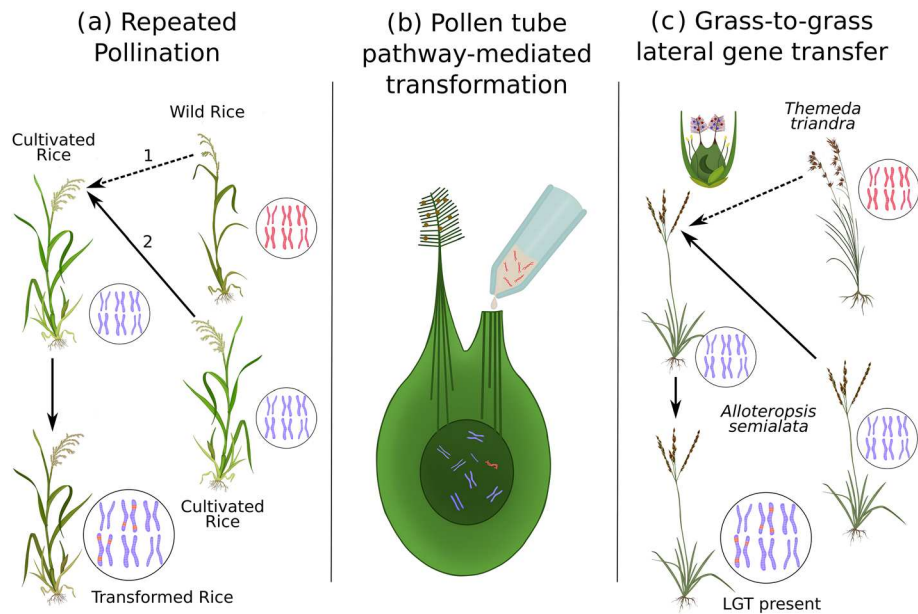


FIGURE 3 Illegitimate pollination methods and how they may facilitate lateral gene transfer (LGT) in the wild. (a) Repeated pollination and (b) pollen tube pathway-mediated transformation are both ways of contaminating the normal reproductive process with small fragments of genomic DNA from a third individual. (a) The repeated pollination example shows cultivated rice first being treated with pollen from the wild relative prior to a second pollination using the same rice cultivar. This results in the transfer of less than 0.1% of genomic DNA from the wild rice (Shan et al., 2005). (b) The pollen tube pathway-mediated transformation example depicts a successfully pollinated style being mechanically cut and exogenous DNA from another species dripped onto the surface. This exogenous DNA is then able to travel along the established pollen tubes and reach the embryos inside the ovary, with approximately 1% of seeds being successfully transformed (Ali et al., 2015). It is possible that these methods are analogous to the mechanism of grass-to-grass LGT (c), with pollen from multiple species present on a single flower facilitating the transfers. In all panels, DNA of the recipient species is shown in blue and the donor in red.

et al., 2015). However, the technique used to search for *Z. latifolia* DNA was genomic in situ hybridization (Silva & Souza, 2013), a cytological method used to identify hybridization or introgression, but which may not be sensitive enough to detect the transfer of small genomic fragments. Whole-genome sequencing data was obtained to analyze TE mobilization, but these data were not employed to search for *Z. latifolia* sequences. Since a chromosome-level reference genome for *Z. latifolia* has become recently available (Yan et al., 2022), it would be interesting to evaluate whether these whole-genome resequencing datasets contain genomic fragments from the donor species. Overall, these experiments prove that the presence of heterospecific pollen from distant species during pollination can promote TE mobilization and transfer of genomic DNA from the donor species in the recipient genome. Although it is not clear where, when, and how the DNA exchanges happen, the presence of foreign pollen is enough to contaminate the reproductive process, without further human intervention.

2.4.2 | Pollen tube pathway-mediated transformation

Pollen tube pathway-mediated transformation is a similarly straightforward approach. It consists of injecting alien DNA at a certain time into the gynoecium in order to transfer it by following the nucellus

pathway of a pollen tube (Figure 3b) (Zhou et al., 1979). The effectiveness of this method was confirmed by isotope tracing using H_3 labeled DNA, demonstrating that heterologous DNA entered the embryo (Gong et al., 1988). Cotton was the first species transformed using the pollen tube pathway-mediated transformation, and for which protocols are specifically optimized (Wang et al., 2013; Zhang et al., 2009), but since then, the method has also been applied to other important species, including certain grasses (Ali et al., 2015). There are three variants of the pollen-tube transformation technique: microinjection of DNA into the ovary, direct delivery of DNA onto the stigma, and pollination with pollen that was previously transformed using other methods (Wang et al., 2013). The exogenous DNA employed for these transformations can be a plasmid or genomic DNA, and ~0.5–1% of the obtained seeds are typically transformed. The success of this method demonstrates that once genomic DNA is present in the pistil, either on the stigma or in deeper layers of the organ, it can be incorporated into the recipient's genome. Remarkably, heterospecific pollen tube growth itself does not seem to be completely essential for transfers, just the presence of DNA fragments.

2.4.3 | Likely occurrence in the wild

Grasses are wind-pollinated meaning that the stigma will indiscriminately receive pollen from co-occurring species. Depending on the

compatibility, these heterospecific pollen grains may germinate and grow to a certain extent. Most of the heterospecific pollen tubes will fail at some point, but a small proportion might reach the micropyle and enter the ovule. Once the sperm cell has been released, pollination could succeed, giving rise to interspecific hybrids (including wide crosses). But even when pollination fails, the exogenous DNA is already present within the ovule, offering opportunities for the integration of DNA segments into the recipient's genome, as shown experimentally in repeated pollination experiments (Figure 3c). In addition, the presence of unsuccessful, degenerative pollen tubes from heterospecific pollen within the style would also lead to the presence of exogenous DNA in the reproductive tissue. This DNA could be inadvertently carried to the ovule by a pollen tube from the same species, as observed in the pollen tube pathway-mediated transformation.

The transformation methods discussed here are relatively simple and do not require *in vitro* culture. There is no reason why the same processes could not lead to transformation of grasses in the wild, underpinning the observed grass-to-grass LGTs. These reproductive contamination transformation mechanisms should therefore be considered as viable mechanisms of LGT in the wild.

3 | HOW IS EXOGENOUS DNA INTEGRATED IN THE HOST GENOME?

Getting DNA into the cell is only half of the story, and to be maintained and passed to future generations, this DNA needs to be incorporated into the recipient's genome. However, this is the easy part, as proven by transformation methods. One of the most successful transformation methods is particle bombardment (Klein et al., 1987), where DNA is mechanically introduced into the cell and subsequently integrated by chance into the recipient genome in a random position. We briefly review some of the potential mechanisms by which this integration could happen.

3.1 | Transposable elements

In plants, transposable elements (TEs) are a major component of genomes, comprising >80% of the genome in some species (Lee & Kim, 2014). These repetitive sequences were overrepresented in laterally acquired DNA identified in several studies (El Baidouri et al., 2014; Fortune et al., 2008; Park et al., 2021; Roulin et al., 2008, 2009). It is possible that endogenous mechanisms of DNA repair and retrotransposon machinery could both play a role in mobilizing exogenous DNA and its subsequent introgression into the host genome. In addition, TEs seem to be involved in repeated pollination experiments, since TE mobilization was the most evident consequence of heterospecific pollination (Shan et al., 2005; Wu et al., 2015). TEs are also activated in response to environmental stresses (Alzohairy et al., 2014) and during reproductive development (Mirouze &

Vitte, 2014), which could facilitate the integration of alien DNA fragments from donor species in these situations.

3.2 | Starships

A novel kind of mobile element, called "starships," has been characterized in fungi as a potential vector for LGT (Gluck-Thaler et al., 2022). Starships are giant elements (>100 kb in some cases) containing a specific, conserved set of genes that allow them to act as a cargo carrier and generate gene content variation in fungi. The existence of Starship elements in plants has not been investigated to our knowledge. If they are present in plant genomes, they would offer another hypothesis to explain the integration of exogenous genes into the host genome.

3.3 | Extrachromosomal circular DNA

LGT requires DNA to be excised from one genome, for it to exist as a stable and mobile intermediate for a prolonged period during transfer, before finally being integrated into the host genome. The known formation mechanism, stability against exonuclease degradation and capacity to reinsert in chromosomes makes extrachromosomal circular DNA (eccDNA) a very good candidate vector (Cohen et al., 2008; Koo et al., 2018). These molecules can also be passed to progeny through a mechanism of chromosome tethering (Koo et al., 2018). Such minicircles, composed of a mix of both viral and plant genomic sequences, have been observed in sugar beet (*Beta vulgaris*) infected by the geminivirus BCTIV (Catoni et al., 2018). Fragments of up to 1 kb of plant DNA were observed in the chimeric eccDNA, although no open reading frame was present. The formation of these circles was observed in experimental sugar beet plants within four weeks of viral inoculation, and although spontaneous formation did not happen in other tested species, the eccDNA were spread and replicated in *Arabidopsis thaliana* and *Nicotiana benthamiana* as a result of subsequent viral infection. If the material from *B. vulgaris* contained in these viral circles were integrated in *Arabidopsis* or *Nicotiana* cells, it would result in an LGT event mediated by eccDNA.

To summarize, it is unlikely that lateral gene transfer is restricted to a particular form of DNA, as we know once genomic DNA is introduced into a cell (e.g., through particle bombardment) it can be incorporated into the host genome. However, properties such as stability and mobility will likely influence the frequency with which transfers are mediated by a particular DNA vector.

4 | FINAL REMARKS

As reports of lateral gene transfer in eukaryotes increase, the skepticism wanes (van Etten & Bhattacharya, 2020), although it has been argued that a well-characterized mechanism is still required

for its universal acceptance as an important force in eukaryotic evolution (Martin, 2017). Here, we specifically address this demand, and review empirical evidence for several mechanisms that could underpin the frequently observed grass-to-grass lateral gene transfers. Multiple mechanisms may play a role, although those that particularly stand out involve illegitimate pollination and reproductive contamination. Repeated-pollination and pollen tube pathway-mediated transformation are both plant transformation methods that can be easily used to contaminate the reproductive process with fragments of foreign DNA from a distantly related species. These methods require minimal human intervention and we see no reason why these processes cannot naturally occur in the wild and facilitate grass-to-grass LGT. While the exact mechanism responsible for documented transfers that occurred during the course of a lineage's evolution is likely to remain unknown, our review of existing experimental approaches shows that viable mechanisms exist.

Finally, much of the research reviewed here is beginning to show that the distinction between what we class as hybridization, transformation, and LGT may be less discrete than we first thought. Hybridization is typically envisaged to be a result of sexual reproduction and the union of two complete sets of chromosomes from female and male gametes, whereas transformation and lateral gene transfer involve the transfer of DNA without sexual reproduction, and the amount of DNA transferred is typically only a small fraction of the donor genome, with laterally transferred DNA fragments up to ~400 kb. These discrete categories are clearly maintained for vector-mediated LGTs when compared to classical hybridization, but what about cases where the transfer explicitly rely on sexual reproduction such as the pollen tube pathway-mediated transformation? LGT and transgenesis are also effectively analogous, with the distinction being whether the process is natural or artificial. But again, it appears that many of the transformation methods without the requirement of in vitro culture may occur naturally, in which case they would be referred to as LGTs, at which point the distinction becomes arbitrary. Indeed, this distinction is likely to become further debated as agricultural biotechnology becomes more widely used and examples of "natural genetic engineering" through LGT increase.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

L.P., P.-A.C., and L.T.D. reviewed the literature and wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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